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Trait differentiation between native and introduced populations of the invasive plant *Sonchus oleraceus* L. (Asteraceae)

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Abstract

There is growing evidence that rapid adaptation to novel environments drives successful establishment and spread of invasive plant species. However, the mechanisms driving trait adaptation, such as selection pressure from novel climate niche envelopes, remain poorly tested at global scales. In this study, we investigated differences in 20 traits (relating to growth, resource acquisition, reproduction, phenology and defence) amongst 14 populations of the herbaceous plant *Sonchus oleraceus* L. (Asteraceae) across its native (Europe and North Africa) and introduced (Australia and New Zealand) ranges. We compared traits amongst populations grown under standard glasshouse conditions. Introduced *S. oleraceus* plants seemed to outperform native plants, i.e. possessing higher leaf and stem dry matter content, greater number of leaves and were taller at first flowering stage. Although introduced plants produced fewer seeds, they had a higher germination rate than native plants. We found strong evidence for adaptation along temperature and precipitation gradients for several traits (e.g. shoot height, biomass, leaf and stem dry matter contents increased with minimum temperatures, while germination rate decreased with annual precipitations and temperatures), which suggests that similar selective forces shape populations in both the native and invad-

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ed ranges. We detected significant shifts in the relationships (i.e. trade-offs) (i) between plant height and flowering time and (ii) between leaf-stem biomass and grain yield between native and introduced plants, indicating that invasion was associated with changes to life-history dynamics that may confer competitive advantages over native vegetation. Specifically, we found that, at first flowering, introduced plants tended to be taller than native ones and that investment in leaf and stem biomass was greater in introduced than in native plants for equivalent levels of grain yield. Our study has demonstrated that climatic conditions may drive rapid adaption to novel environments in invasive plant species.

Keywords

Agricultural weed, Common sowthistle, ecological trade-offs, plant trait differentiation, Rapid trait evolution

Introduction

Introduced plant species are a threat to native biodiversity (Hejda et al. 2009; Pyšek et al. 2012) and drive considerable economic costs associated with their management and reduced agricultural yields (Hoffmann and Broadhurst 2016). According to a recent review, about 4% of vascular plant species have become naturalised beyond their native range (van Kleunen et al. 2018), with the highest densities of naturalised plant species recorded for Pacific Islands (van Kleunen et al. 2015; Essl et al. 2019). There are several mechanisms by which alien plants can become invasive after introduction to a novel range. An understanding of why some plants become invasive is essential to prioritise their management. For example, interactions between the introduced propagules and the resident plant species of the novel environment may account for invasion success (Catford et al. 2009). Escape from specialist enemies (e.g. herbivores and pathogens) in the introduced range may enhance the survivorship and competitive performance of alien plants, as proposed by the Enemy Release Hypothesis (Darwin 1859; Keane and Crawley 2002). Damage induced by natural enemies are then reduced in the introduced range compared to the native range (e.g. Meijer et al. 2016).

Adaptation to novel environmental conditions, through rapid evolution resulting in phenotypic changes (Oduor et al. 2016; van Kleunen et al. 2018), may also account for successful plant invasion (Prentis et al. 2008; Colautti and Lau 2015; Stutz et al. 2018). Several recent studies have shown that alien plants can undergo rapid evolution through trait adaptation to novel selection pressures (e.g. Molina-Montenegro et al. 2018; van Boheemen et al. 2019a; Lustenhouwer et al. 2019; Brandenburger et al. 2019a, b). Rapid trait adaptation may be driven by several processes; for example, the Evolution of Increased Competitive Ability (EICA) hypothesis posits that there is an evolutionary shift from costly defensive abilities to competitive performance in introduced populations, due to the absence of co-introduced specialist enemies (Blossey and Notzold 1995). Despite evidence for differences in several growth and defence traits between native and introduced populations (e.g. Felker-Quinn et al. 2013; Colautti and Lau 2015; Rotter and Holeski 2018; van Boheemen et al. 2019b), some meta-analyses have reported that the EICA hypothesis is only partially supported (Felker-Quinn et al. 2013; Rotter and Holeski 2018).

Other traits relating to plant phenology (Turner et al. 2014) and resource acquisition efficiency (e.g. specific leaf area, leaf and stem dry matter content, carbon to nitrogen ratio of seeds and leaves, Wright et al. 2004; Grassein et al. 2010)) have also been shown to rapidly change following introduction as a result of competition for novel resources (Gioria and Osborne 2014; Lustenhouwer et al. 2019). Many recent studies have shown that climate niche envelopes occupied by invasive plants in their introduced ranges can differ substantially to native ranges and exposure to novel climatic regimes may select for divergent traits of alien plant populations (Early and Sax 2014; Moran and Alexander 2014; van Boheemen et al. 2019a). Indeed, rapid adaptive evolution has been observed along latitudinal and longitudinal gradients in response to variations in temperature and precipitation (e.g. Callaway and Maron 2006; van Kleunen and Fischer 2008; Colautti et al. 2009; Alexander et al. 2012). However, it remains poorly understood at global scales whether the degree to which trait differences between native and introduced ranges are modulated by novel climate regimes and whether such traits confer fitness benefits (and thus invasion potential) to the introduced plant populations.

Classical functional ecological theory posits that plant growth, reproduction and defence may be traded-off or partitioned along competition, stress and disturbance gradients (e.g. Reekie and Bazzaz 1987; Stearns 1989; Edward and Chapman 2011), especially when resources (e.g. nutrients) are limiting (Grime 2006). It has been suggested that these trade-offs and their response to changing environmental factors, play a crucial role in invasion success of alien plants (Beckmann et al. 2009; Forrest and Miller-Rushing 2010; Colautti et al. 2010, 2017; Anderson and Gezon 2015). For example, some introduced species can overcome trade-offs in growth and reproduction by producing large numbers of flowers in dense populations under high competition (Lambrecht-McDowell and Radosevich 2005; Beckmann et al. 2009; Weiner et al. 2009). Trade-offs can also occur between timing of flowering and plant size at time of reproduction. Plant phenology is highly constrained by environmental selection pressures (e.g. climate, resources, disturbances) (Forrest and Miller-Rushing 2010). Reproductive effort, as measured by flower production, can often be determined by a "time-size" trade-off that balances the advantages of early reproductive maturity versus greater growth prior to fruit production (Bolmgren and Cowan 2008). Earlier flowering implies the allocation of fewer resources to maternal plant growth, resulting in smaller plants at flowering (Vile et al. 2006). The resources saved in this manner are instead invested in offspring development (Bolmgren and Cowan 2008). However, there is little knowledge about how trade-offs between key functional traits associated with growth and reproduction vary between native and introduced populations of introduced species or their contribution to invasion success.

The aim of this study was to investigate differences in plant functional traits associated with growth, resource acquisition, reproduction, phenology and defence between native and introduced populations of the common sowthistle, *Sonchus oleraceus* L. (Asteraceae) across temperature and precipitation gradients. This species is a herbaceous plant native to Europe (Gleason and Cronquist 1991), North Africa and West Asia (Peschken 1982) that was introduced to the islands of Oceania (i.e. Australia and

New Zealand) in the late 18th century (Boulos 1974; Prebble 2008). It is now the most widely distributed plant species around the globe (present on 48% of emerged land) (Pyšek et al. 2017).

Field-based trait measurements can determine how plants respond to environmental change *in situ* but cannot discriminate between phenotypically plastic versus genetic responses to local conditions (Montesinos and Callaway 2018; Brandenburger et al. 2019a). For invasive species, adaptive genetic responses in their introduced ranges can be identified using common garden experiments, whereby seeds sourced from native and introduced locations are propagated and grown under standard conditions (e.g. Stutz et al. 2018). Such experiments can control the confounding effects of phenotypically plastic responses to novel environmental conditions observed in the field (Hierro et al. 2005). In this study, we examined the variation in 20 traits associated with growth, resource acquisition, reproduction, phenology and defence between native and introduced populations of *S. oleraceus* using a common garden experiment. The specific objectives were to assess whether (1) the traits of *S. oleraceus* plants differ between native and introduced populations, (2) variation in traits is related to climatic conditions and (3) there has been a shift in trade-offs between reproduction and growth between native and introduced populations. We hypothesised that introduced *S. oleraceus* plants would display enhanced growth, more efficient resource use and higher reproductive output, as well as delayed maturity and weaker physical defences, compared with plants from the native range. We also predicted that offspring traits would vary along temperature and precipitation gradients experienced by parent plants, but we had no *a priori* expectation about the direction of these relationships or whether they would vary between native and introduced populations.

Materials and methods

Biological study system

Sonchus oleraceus is an annual, or occasionally biennial species, that has expanded across most of Australia, becoming established in more than 4.3 M ha of crops (cereals and cotton) and fallow land in south-eastern Queensland and northern New South Wales, in particular, where it causes an estimated annual loss of AUD $ 6.3 M (Walker et al. 2005; Osten et al. 2007; Llewellyn et al. 2016). *Sonchus oleraceus* is a ruderal species found primarily in disturbed, open habitats, such as gardens, crops and fallows, including roadsides (Hutchinson et al. 1984). It has been suggested that the spread of *S. oleraceus* in Australia has been favoured by the expansion of no-till agricultural practices (Chauhan et al. 2006) and the emergence of resistance to some herbicides, such as glyphosate (Boutsalis and Powles 1995; Adkins et al. 1997; Cook et al. 2014; Meulen et al. 2016).

Collection of seeds

Seeds were collected from 2016 to 2018, from 14 field populations across two geographic ranges: the native range in the Western Palaearctic (Europe and North Africa) and the introduced range in Oceania (Australia and New Zealand) (Figure 1). We are aware that this sampling does not entirely cover the native area of *S. oleraceus,* but populations were collected from a diverse range of climatic and geographic contexts. Furthermore, preliminary genetic analyses on European (including populations from Great Britain) and Australian populations indicated that the Australian populations were genetically more similar to populations from Southern Europe than to those from Great Britain (CSIRO 2018). One flower head (i.e. capitulum), containing fully ripe seeds (i.e. achenes) with a well-developed pappus, was sampled from each of 14 separate mature *S. oleraceus* plants within each of the 14 populations (i.e. 196 flower heads in total). Seeds were stored for up to two years in paper bags at a constant room temperature (~22 °C) with silica gel until sowing.

Within the native range, a collection permit was obtained for Andalusia (Spain) (ID: 64oxu764FIRMAF+xU9RItQJeLhEPV, 05/12/2017). No specific permission was required for seed sampling at other sites in Europe and North Africa or for seeds collected in Australia and New Zealand. No specific authorisation was required to introduce seeds into France.

Cultivation of plant material

Plant propagation and common garden growth experiments were performed in a glasshouse at the CSIRO European laboratory in Montpellier, France. In March 2018, eight seeds from each flower head (i.e. 1,568 in total) were sown on moistened Whatman® filter paper on a substrate of vermiculite in a Petri dish. Seeds were maintained in

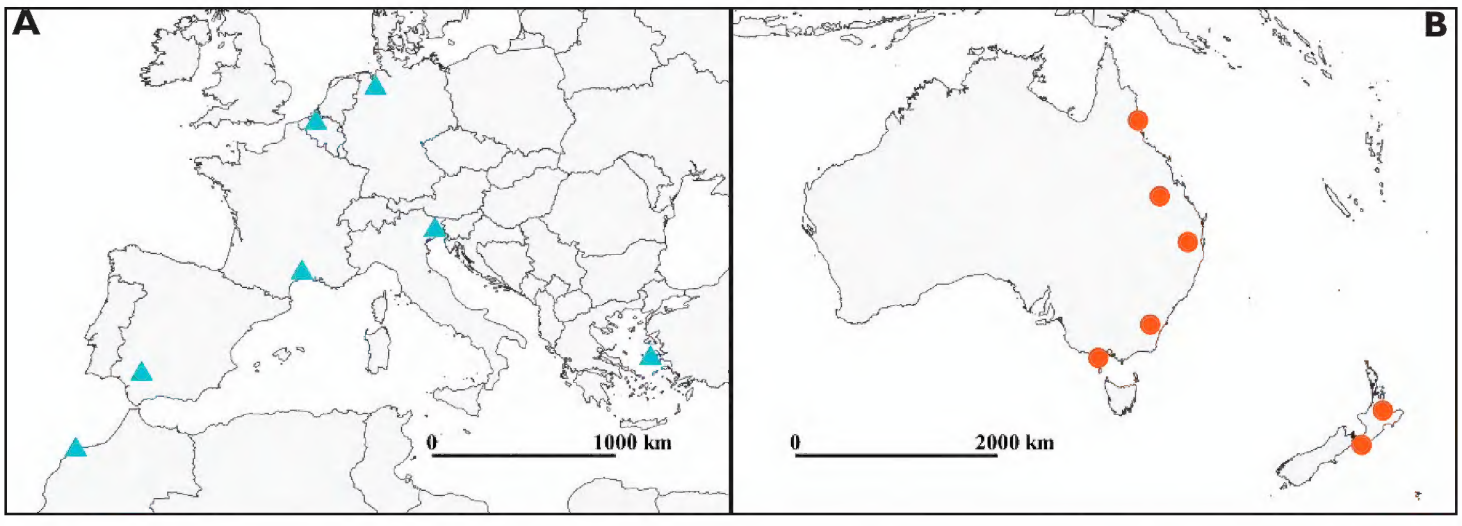

Figure 1. Maps of the collection locations for *Sonchus oleraceus* seeds across (**A**) the native range in Europe and North Africa (blue triangles) and (**B**) the introduced range in Australia and New Zealand (orange circles).

a growth room at a temperature of 25 °C/20 °C (day/night) to stimulate germination. Seven days after sowing, three seedlings per flower head were planted in a single pot (upper diameter ~ 16 cm, height ~ 19 cm) filled with 1.15 kg of nursery-grade soil ("Terreau à mottes Neuhaus, Humin-Substrat N2", ratio of N:P:K = 14:16:18). Pots were transferred to a glasshouse with a minimum night-time temperature of ~15 °C and maximum daytime temperature of ~32 °C. Pots were arranged in a standard Latin square design, such that plants derived from each source population were present once in each row and once in each column. Twelve days after planting, two seedlings were removed from each pot, leaving a single target plant, which was used for growth and functional trait measurements. All plants were watered two to three times per week, with equal volumes of tap water (i.e. between 100 and 400 ml). All plants were sprayed with a sulphur solution (Sulfostar, BASF) every two weeks, to control powdery mildew infestation. Pots were redistributed within the glasshouse at random every three days, to account for variability in light exposure.

Measurement of plant traits

We measured 20 traits (from five categories: growth, resource acquisition, reproduction, phenology and defence) at different stages of plant development on 194 replicates (two plants died during the experiment) between March and July 2018.

Growth traits. We first determined the height of each *S. oleraceus* plant when the first flower bud appeared, measured as the distance (cm) between the soil surface and the first cauline leaf at the base of the inflorescence. As described by Bolmgren and Cowan (2008), we considered this vegetative height measurement to correspond to the point at which investment in the growth of the maternal plant body switched to investment in reproductive output. We ended the experiment after ~80 days when each of the 194 plants had produced seeds from at least five flower heads and begun senescing. At this point, we measured maximum shoot height (cm) from the base of the soil to the top of the tallest flower head and above-ground biomass (g) after oven-drying at 70°C for 72 h. After 80 days, the phenological stage might have differed slightly between plants, raising questions about the influence of the phenological stage on maximum shoot height and above-ground biomass. Although significant for dry biomass, no strong correlation was found between these two traits and days to flowering (dry biomass: $R^2 = 0.024$, $F_{(1,188)} = 4.706$, *p value* = 0.031 and shoot height: $R^2 = 0.019$, $F_{(1,189)} = 3.819$, *p value* = 0.052), demonstrating their independence from plant phenology and validating their use for plant comparisons.

Resource acquisition traits. Basal leaves (forming a rosette) capture light and synthesise chemical energy to support the growth of stem, cauline leaf and reproductive tissues (Cici et al. 2009). We therefore used the basal leaves to assess leaf resource acquisition (associated with light interception and photosynthate assimilation). The largest basal leaf on each plant was sampled when the first flower bud emerged. Each leaf was placed in a test tube filled with deionised water and was stored in the dark

for 24 h at 4°C. We measured the fresh weight (g) and surface area (cm^2) of each rehydrated leaf with an Epson Perfection V550 Photo digital image scanner, processing the images obtained with WinFOLIA software. Leaf dry mass (g) was then determined by drying the leaves in an oven at 70°C for 72 h. Specific leaf area (SLA) was calculated as the ratio of leaf surface area to dry mass (m^2/kg; Pérez-Harguindeguy et al. 2013). Leaf dry matter content (LDMC) was calculated as the ratio of dry mass to rehydrated fresh mass (mg/g; Pérez-Harguindeguy et al. 2013). Leaf thickness (μm) was estimated with the equation proposed by Vile et al. (2005): [1/(SLA × LDMC)], which provides a good approximation for thickness in laminar leaves (Pérez-Harguindeguy et al. 2013). We estimated the overall potential of the plant for light interception and photosynthate assimilation by counting the total number of leaves produced by the time the first flower bud had emerged. At the end of the experiment, we also calculated LDMC for the first cauline leaf located at the base of the inflorescence and stem dry matter content (SDMC, mg/g) for a 5 cm-long piece of stem. Carbon-to-nitrogen ratio (C:N) was measured on the basal leaves and seeds of glasshouse plants at the end of the experiment with an elemental analyser (model EA 1108; Carlo Erba Instruments, Milan, Italy), after the plant materials had been dried at 70°C for 72 h.

Reproductive traits. We first calculated the viability of field-collected seeds as the proportion of the seeds sown that germinated at three and six days after sowing. We chose to measure germination at two time points, as we had no preconceived notions about potential differences in germination rates between the two ranges. On average, 75-80% of the seeds had germinated after six days (Suppl. material 2, Table S2). At this time point, the seeds that had not germinated tended to become soft, discoloured and started to rot, indicating that they were not viable (see Edwards et al. 2019). Over the course of the experiment, we counted the total number of flower heads longer than 5 mm per plant. The mean number of seeds per flower head and mean seed mass (μg) per plant were estimated from the mean dry weight (μg) of 100 seeds for five flower heads. We also determined the seed dispersal potential (termed the seed dispersal window), as the difference (cm) between the highest and lowest flower heads on each inflorescence per plant. Previous studies have shown that plant height during seed production is strongly related to seed dispersal distance (Thomson et al. 2011). However, we found that flower heads were widely spread across inflorescences, so a single measurement of the highest flower head would not adequately represent the breadth (or window) of dispersal opportunities for the plant.

Phenological traits. We measured two phenological traits associated with the timing of key reproductive stages: we counted the number of days until development of the first flower bud (longer than 5 mm) and the number of days until the emergence of the first fully-open flower head.

Defence traits. We characterised investment in defence against generalist herbivores (Hanley et al. 2007), by visually recording the number of trichomes in two 1 cm^2 quadrats (one on the upper surface and one on the lower surface) at the distal tip of a single basal leaf per plant.

Climatic data for the original locations of the populations

We evaluated the effects of two climate variables on each of the 20 functional traits considered: mean minimum temperature of the coldest month and mean annual precipitation, calculated from 1970 to 2000 (Supplementary material S1). Data were retrieved from WorldClim with the 'raster' package (Hijmans et al. 2019) and R software (R Core Team 2018). We selected these two variables, based on the extensive overlap of values between native and introduced regions and the absence of interdependence between them (R^2 = 0.004, $F_{(1/194)}$ = 0.127, *p value* = 0.723). We also tested mean maximum temperature of the warmest month, but we did not retain this variable for the analysis because it was correlated with the other selected variables (maximum temperature and precipitation: R^2 = 0.23, $F_{(1/194)}$ = 57.96, *p* value < 0.001; maximum temperatures and minimum temperatures: R^2 = 0.18, $F_{(1/194)}$ = 45.19, *p* value < 0.001).

Trade-offs between traits associated with growth and reproduction

We investigated differences between native and introduced populations in two resource allocation trade-offs related to growth and reproductive effort: *i.e.* relationships (1) between time to flowering and vegetative height at first flower bud and (2) between grain yield and leaf-stem biomass. Grain yield represents an aggregate measure of reproductive effort (Donald and Hamblin 1976; Unkovich et al. 2010). Estimates of grain yield and leaf-stem dry biomass were obtained as follows:

1) Grain yield (g) = seed mass (g) * number of seeds per flower head * number of flower heads per plant
2) Leaf-stem dry biomass (g) = total above-ground dry biomass (g) – grain yield (g)

Statistical analyses

As a first step, we performed a phylogenetic principal component analysis (PCA) incorporating the 20 traits to explore the multidimensional distribution of individual plants from native and introduced ranges, based on the entire suite of traits. The phylogenetic PCA was used, because it accounts for the non-independence of plants derived from the same source population (Revell 2009). We used the R package phytools (function *phyl.pca*) (Revell 2012) for the analysis. To perform this phylogenetic PCA, we provided, as an additional dataset, a phylogenetic tree depicting the relationships amongst individuals derived from the same source population (i.e. the tree is composed of 14 clades, each containing 14 individuals, simply coded as 14 vectors of the 14 plant identification numbers and was built using *read.tree* and *compute.brlen* func-

tions). We excluded data for 24 plants from the analysis due to incomplete measurements for some leaf traits as a result of the samples being damaged (i.e. we analysed n = 170 plants). The missing data were evenly distributed between the populations and concerned ten traits (days to flowering, SLA, thickness, basal LDMC, SDMC, shoot height, dispersal window, number of seeds, seed mass and seed and leaf C:N ratios). As an overall approach to distinguishing plants between specimen areas of origin, we performed tests with individual coordinates on the first and second dimensions of the PCA. As the coordinates of dimension 1 were not normally distributed, we analysed it with a Mann-Whitney non-parametric test. The coordinates of dimension 2 were approximately normally distributed and were therefore analysed with a one-way parametric ANOVA.

We used mixed models to test for differences in each plant trait between native and introduced ranges. Linear mixed models (LMM) were used for continuous data, such as masses and lengths. For C:N ratios of leaves, data were log-transformed to meet the requirement of a normal distribution of residuals. Generalised linear mixed models (GLMM) were used for discrete variables, such as counts (Poisson distribution), percentages (binomial distribution) and duration (Gamma distribution). Range of origin was considered as a fixed factor, whereas population of origin within each range was considered as a random categorical predictor variable. For each trait, the bench, on which the plants were placed in the greenhouse, was tested as a random factor, but was subsequently removed from the model as it was found to have no effect, confirming the successful randomisation of the experiment. Previous research by Hutchinson et al. (1984) and Widderick et al. (2010) showed that the half-life of mature *S. oleraceus* achenes is up to 3 years under dry storage conditions, with no effect on seed viability or "germinability". To confirm this assumption, we tested the effect of year-of-seed collection on germination rate by including this variable as a covariate predictor in models (Suppl. material 1, Table S1). No significant effect of year of collection was observed (germination rate after 3 days: LRTχ^2 = 0.69, df = 2, p *value* = 0.71, germination rate after 6 days: LRTχ^2 = 0.36, df = 2, p *value* = 0.83), so this covariate was removed from the models for further traits tested.

We then accounted for the possible influence of climatic conditions on trait differences between native and introduced populations using a second series of mixed models that included the two climate covariates: mean minimum temperature of the coldest month and mean annual precipitation. The interaction of range with each of the covariates was also considered, as traits might respond differently to climate between ranges. For both series of mixed models (with and without climatic covariates), the significance of each main effect or interaction was assessed in a stepwise manner, using likelihood ratio tests (LRTs). The proportion of the variance explained by each full model (i.e. R^2 values) is reported (Nakagawa and Schielzeth 2013). When using LRTs, since it is not meaningful to test the significance of main effects that are included in significant interactions ($p < 0.5$), the main effects were not tested but were retained in the model as recommended by Floyd and Gurevitch (1997).

We finally investigated whether the trade-offs between flowering time and vegetative height at time of reproduction and between leaf/stem biomass and grain yield differed between native and introduced plant populations. We performed two analyses of covariance (ANCOVA) for each of the trait combinations, considering the predictor variable and range as fixed factors and population of origin as a random covariate. We accepted the hypothesis (i.e. that the trait associations differ between native and introduced ranges), based on significant interaction terms in each model along with different slopes of regression lines. Interactions were tested by comparing two different models (with and without the interaction term) in LRTs. Both trade-offs are plotted to illustrate the correlation patterns by range.

All analyses were performed with the software R (R Core Team 2018). The "nlme" package (function *lme*) was used for linear mixed models and the "lme4" package (function *glmer*) was used for generalised linear mixed models. For mixed models, R^2 was obtained with the "piecewiseSEM" package (function *rsquared*).

Results

Difference in *S. oleraceus* traits between native and introduced ranges without taking climatic covariates into account

The first two principal component axes of the phylogenetic PCA accounted for 34.53% of the variance (Figure 2). Axis 1 was inversely correlated with phenological traits (days to first flower bud and days to flowering), height at first flower bud and leaf C:N ratio. Axis 2 was weakly positively correlated with SLA of basal leaves and inversely correlated with biomass, SDMC and LDMC of cauline leaves. The confidence ellipses (Figure 2) revealed a large overlap between native and introduced plants, although there appeared to be some differentiation between a few specimens along Axis 2. No significant differences between the two ranges was observed for the first component co-ordinates ($W = 3069$, p value = 0.12), but a significant difference between the two ranges was detected for the second component (F value = 8.37, $df = 1$, p value < 0.01). Introduced plants tended to have a higher biomass, SDMC and LDMC of cauline leaves and a lower SLA of basal leaves. However, the low proportion of the variation, accounted for by the first two dimensions, highlighted the need to test the effect of range for each trait independently.

Regarding growth traits (Figure 3, Supplementary materials S2, S3), vegetative height at first flower bud and the above-ground dry biomass of the plant were both significantly higher for introduced than for native plants ($LRT\chi^2 = 3.857$, $df = 1$, p value = 0.049 and $LRT\chi^2 = 4.885$, $df = 1$, p value = 0.027, respectively). For resource acquisition traits, significantly higher values were observed for introduced plants for the number of leaves at first flower bud and SDMC ($LRT\chi^2 = 9.687$, $df = 1$, p value = 0.002 and $LRT\chi^2 = 7.955$, $df = 1$, p value = 0.005, respectively). None of the other traits differed significantly between the two ranges (all p values > 0.05).

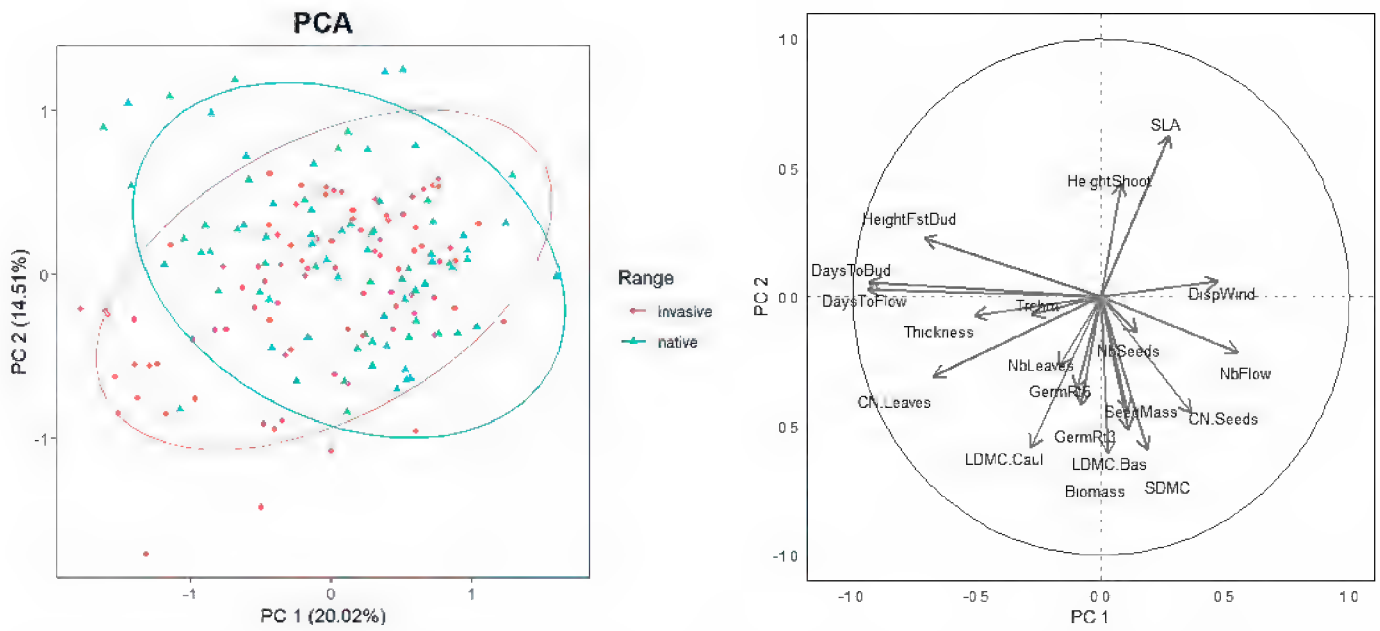

Figure 2. Phylogenetic principal component analysis (PCA) plot, based on individual values for 20 traits measured in 14 populations of *Sonchus oleraceus* from the native (Europe and North Africa, blue triangles) and introduced (Australia and New Zealand, orange circles) ranges. The 95% confidence ellipses, defined by the centre of gravity of each range, are represented. The first two components account for 34.53% of the total variance. On the right, is presented the correlation circle on the 20 variables represented by the two principal components (*HeightFstBud*: vegetative height at first bud, *HeightShoot*: total shoot height, *Biomass*: biomass, *SLA*: SLA, *LDMC.Bas*: LDMC of basal leaf, *LDMC.caul*: LDMC of cauline leaf, *Thickness*: leaf thickness, *NbLeaves*: number of leaves, *SDMC*: SDMC, *CN.leaves*: C:N ratio of leaves, *CN.seeds*: C:N ratio of seeds, *GermRt3*: rate of germination at three days, *GermRt6*: rate of germination at six days, *NbFlow*: number of flower heads, *NbSeeds*: number of seeds, *DispWind*: seed dispersal window, *SeedMass*: seed mass, *DaysToBud*: number of days to bud formation, *DaysToFlow*: number of days to flowering, *Trchm*: leaf trichome density).

Interactive effects of climate and range of origin on plant trait variation

The conclusions drawn after adjustment for bioclimatic covariates were different from those for the previous analysis (Table 1). For growth traits, a significant interaction was observed between range and minimum temperature for vegetative height at first flower bud (Figure 4). The height of the introduced plants increased with increasing minimum temperature, whereas no such relationship was observed for native plants. Total shoot height was significantly influenced by minimum temperature (increasing with increasing minimum temperature), but no significant differentiation was observed between ranges (Table 1). The above-ground dry biomass did not differ significantly between ranges, although it was significantly positively associated with minimum temperature across both ranges (Table 1).

Regarding resource acquisition traits, LDMC of cauline leaves, number of leaves and SDMC differed significantly between native and introduced plants (Table 1). Cauline LDMC was ~10% higher for introduced plants, as were the number of leaves by ~38% and SDMC by ~10%. Cauline LDMC and SDMC were also positively influenced by minimum temperature (Table 1). A significant interaction between range and minimum temperature was detected for seed C:N ratio (Figure 4), which increased with increasing temperature for introduced plants, but decreased with in-

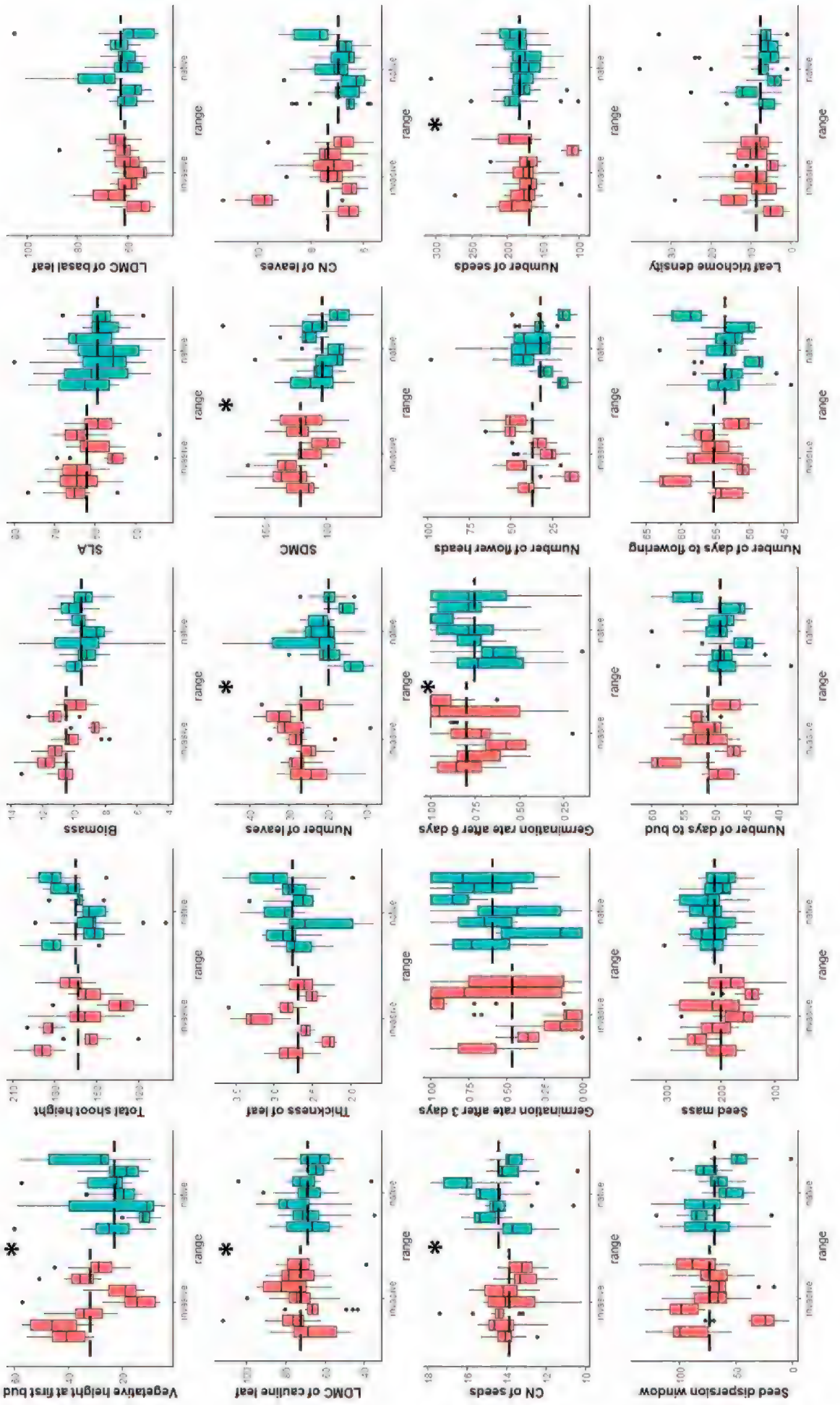

Figure 3. Box plots for twenty traits measured in native (Europe and North Africa, blue) and introduced (Australia and New Zealand, orange) *Sonchus oleraceus* plants, grown under standardised conditions. Growth: vegetative height at first bud (cm), total shoot height (cm), biomass (g). Resource acquisition: SLA (m^2/kg), LDMC of basal and cauline leaves (mg/g), leaf thickness (µm), number of leaves, SDMC (mg/g), C:N ratio of leaves, C:N ratio of seeds. Reproduction: rate of germination (0 to 100%) at three and six days, number of flower heads, number of seeds, seed dispersal window (cm), seed mass (µg). Phenology: number of days to bud formation, number of days to flowering, defence: leaf trichome density (trichomes/cm^2). The dashed horizontal lines through boxplots indicate the mean for each range. Asterisks indicate a significant difference between ranges (as main effect or in interaction with one of the climatic variables).

Table 1. Results of mixed models assessing the effect of range (native: Europe and North Africa, introduced: Australia and New Zealand), two climatic covariates (mean minimum temperature of the coldest month and mean annual precipitation) and their interaction (the population within a range being considered as a random factor), for 20 plant traits measured on *Sonchus oleraceus* under standardised conditions.

Response variable	**Main effect**			**Interaction**		R^2	
Trait	Range	Minimum temperatures	Annual precipitation	Range: Min. temp.	Range: An. Prec.		
	LRTχ^2 (*df*) *p*	*LRT*χ^2 (*df*) *p*	*LRT*χ^2 (*df*) *p*	*LRT*χ^2 (*df*) *p*	*LRT*χ^2 (*df*) *p*	R^2m	R^2c
Growth							
Vegetative height at first bud	nt	nt	0.20 (1) *0.66*	4.04 (1) ***0.04*** *	0.20 (1) *0.66*	0.20	0.42
Total shoot height	1.11 (1) *0.28*	6.54 (1) ***0.01*** *	0.01 (1) *0.92*	2.80 (1) *0.09* •	0.16 (1) *0.69*	0.21	0.52
Biomass	1.26 (1) *0.26*	12.04 (1) ***<0.001*** ***	3.78 (1) *0.05* •	0.65 (1) *0.42*	0.17 (1) *0.68*	0.31	0.39
Resource acquisition							
SLA	0.74 (1) *0.39*	3.18 (1) *0.07* •	0.56 (1) *0.45*	0.21 (1) *0.65*	1.33 (1) *0.25*	0.06	0.09
LDMC of basal leaf	0.30 (1) *0.58*	1.45 (1) *0.23*	0.89 (1) *0.34*	0.43 (1) *0.51*	1.31 (1) *0.25*	0.06	0.23
LDMC of cauline leaf	6.14 (1) ***0.01*** *	4.11 (1) ***0.04*** *	1.13 (1) *0.25*	2.91 (1) *0.08* •	0.88 (1) *0.34*	0.06	0.07
Leaf thickness	0.01 (1) *0.93*	3.77 (1) *0.05* •	0.14 (1) *0.71*	0.08 (1) *0.77*	0.05 (1) *0.83*	0.12	0.41
Number of leaves	8.99 (1) ***<0.01*** **	2.28 (1) *0.13*	0.71 (1) *0.40*	0.23 (1) *0.63*	2.75 (1) *0.10*	0.33	0.52
SDMC	4.34 (1) ***0.04*** *	0.54 (1) ***<0.01*** **	2.07 (1) *0.15*	0.19 (1) *0.66*	0.37 (1) *0.54*	0.26	0.32
C:N ratio of leaves	1.17 (1) *0.28*	0.98 (1) *0.32*	0.01 (1) *0.92*	0.22 (1) 0.64	0.11 (1) *0.74*	0.06	0.40
C:N ratio of seeds	nt	nt	0.13 (1) *0.71*	4.84 (1) ***0.03*** *	0.15 (1) *0.69*	0.16	0.27
Reproduction							
Germination rate at 3 days	0.23 (1) *0.63*	1.90 (1) *0.17*	5.46 (1) ***0.02*** *	1.48 (1) *0.22*	0.94 (1) *0.33*	0.11	0.52
Germination rate at 6 days	11.30 (1) ***<0.001*** ***	10.77 (1) ***<0.001*** ***	11.25 (1) ***<0.001*** ***	0.31 (1) *0.58*	0.65 (1) *0.42*	0.07	0.20
Number of flower heads	0.25 (1) *0.62*	0.03 (1) *0.86*	0.09 (1) *0.76*	0.36 (1) *0.55*	1.32 (1) *0.25*	0.02	0.46
Number of seeds	nt	0.35 (1) *0.56*	nt	0.86 (1) *0.35*	5.21 (1) ***0.02*** *	0.54	0.66
Seed dispersal window	0.06 (1) *0.80*	3.06 (1) *0.08* •	0.19 (1) *0.67*	0.42 (1) *0.52*	1.16 (1) *0.28*	0.09	0.37
Seed mass	0.03 (1) *0.87*	0.02 (1) *0.89*	1.86 (1) *0.17*	1.72 (1) *0.19*	1.67 (1) *0.20*	0.05	0.22
Phenology							
Number of days to bud	0.93 (1) *0.34*	1.15 (1) *0.28*	0.05 (1) *0.82*	0.13 (1) *0.72*	0.14 (1) *0.71*	0.13	0.29
Number of days to flowering	0.85 (1) *0.36*	1.10 (1) *0.29*	0.04 (1) *0.84*	0.04 (1) *0.84*	0.16 (1) *0.69*	0.12	0.28
Defence							
Leaf trichome density	0.05 (1) *0.82*	1.49 (1) *0.22*	3.59 (1) *0.06* •	0.05 (1) *0.83*	1.37 (1) *0.24*	0.15	0.32

χ^2, chi-squared test statistic; *df*, degrees of freedom; nt, not tested, because of significant interaction term ($p < 0.05$).
The significance of a term is indicated by symbols: •, $p < 0.1$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.
R^2m, R^2 marginal (variance explained by fixed factors only); R^2c, R^2 conditional (variance explained by fixed and random factors).

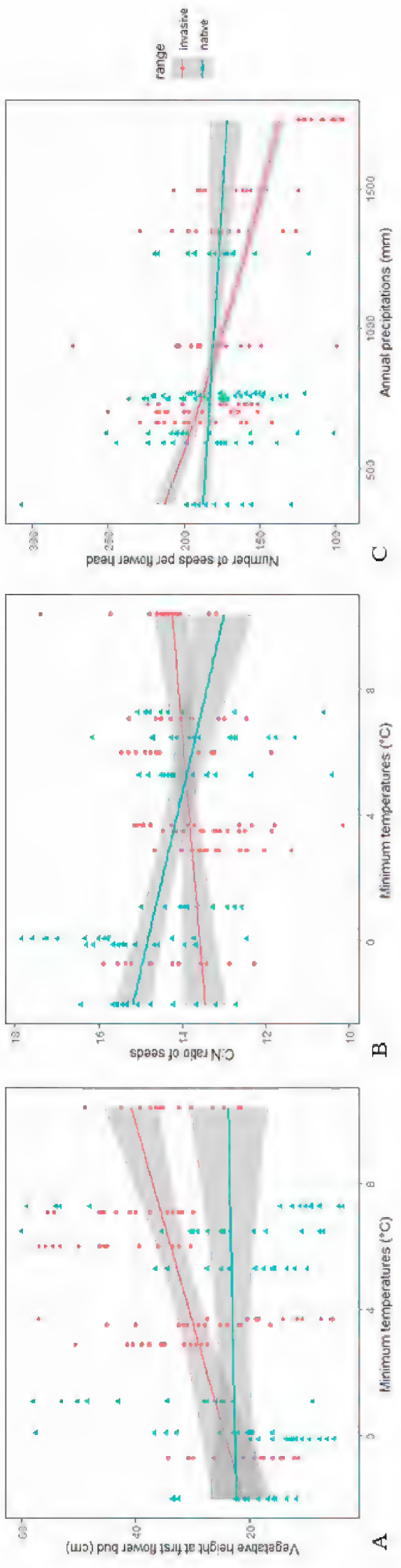

Figure 4. Significant interactions between range of origin (native: Europe and North Africa, introduced: Australia and New Zealand) and climatic conditions (mean minimum temperature of the coldest month and mean annual precipitation) for A) Vegetative height at first flower bud ($LRT\chi^2 = 4.04$, $df = 1$, $p\ value = 0.04$), B) Carbon-to-nitrogen ratio of seeds ($LRT\chi^2 = 4.84$, $df = 1$, $p\ value = 0.03$) and C) Mean number of seeds per flower head ($LRT\chi^2 = 5.21$, $df = 1$, $p\ value = 0.02$).

creasing temperature for native plants. None of the other resource acquisition traits responded significantly to range or bioclimatic covariates.

Amongst reproduction traits, the rate of germination after three days was negatively influenced by annual precipitation but did not differ between ranges (Table 1). However, the rate of germination after six days differed significantly between native and introduced plants, being ~28% higher for introduced plants and was negatively influenced by temperature and precipitation (Table 1). For the number of seeds per flower head, a significant interaction was observed between range and precipitation (Figure 4), with introduced plants tending to display a faster decrease in seed production with increasing precipitation than native plants. None of the other reproductive traits responded significantly to the factors tested.

No significant difference between ranges or influence of climatic conditions was detected for phenological traits (number of days to bud formation and number of days to flowering) and the defence trait (leaf trichome density) (Table 1).

Shifts in trade-offs between native and introduced ranges

The overall relationship between the number of days to flowering and vegetative height at first flower bud was strongly significant ($LRT\chi^2 = 112.74$, $df = 1$, p *value* < 0.001, Figure 5.A). However, the gradient of the relationship differed between native and introduced plants, as indicated by the significant interaction with range in the ANCOVA (significant interaction, $LRT\chi^2 = 12.35$, $df = 1$, p *value* < 0.001). For plants producing their first bud before 55 days, introduced plants tended to be taller than native ones. This difference ceased to be significant for plants that flowered later (indicated by overlapping standard errors and intersecting regression lines, Figure 5.A).

Overall, there was also a very strong negative association between grain yield and leaf/stem biomass ($LRT\chi^2 = 19.33$, $df = 1$, p *value* < 0.001); however, this relationship differed strongly between native and introduced plants (significant interaction term, $LRT\chi^2 = 6.81$, $df = 1$, p *value* < 0.01). For low grain yield (below about 1.75 g per plant), introduced plants invested more resources than native plants in leaf and stem tissues. For grain yields greater than 1.75 g, this difference was no longer significant (overlapping standard errors and intersecting regression lines, Figure 5.B).

Discussion

When considering the full suite of traits, we found that there were only moderate differences in *S. oleraceus* populations between native and introduced ranges (as illustrated by the PCA). Native and introduced plants differed for seven of the 20 traits considered. Three of the seven significant traits were associated with resource acquisition, with higher values obtained for introduced plants (higher leaf and stem dry matter content, larger number of leaves). Climatic conditions significantly influenced nine

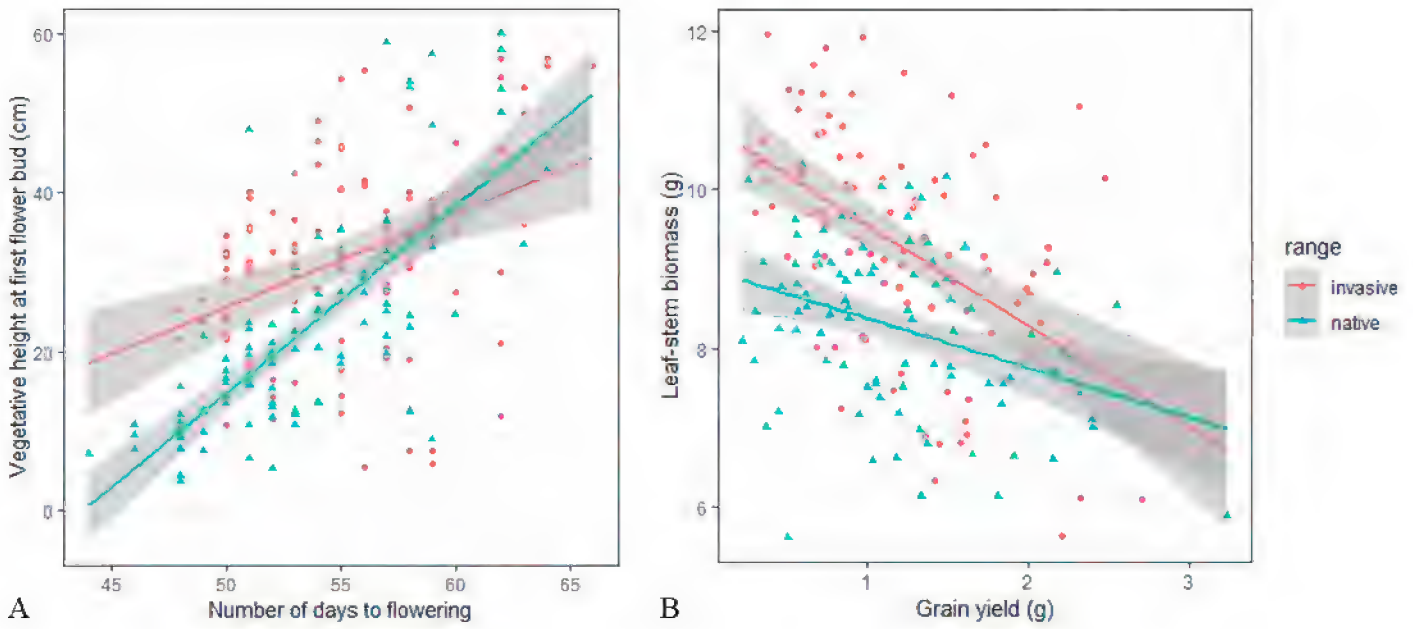

Figure 5. Significant shift in trade-offs between native and introduced populations. **A** Relationship between vegetative height at first flower bud (cm) and number of days to flowering for *Sonchus oleraceus* populations in the native range (West Palearctic, blue) and in the introduced range (Oceania, orange). Regression estimates for native plants: $y = 2.35\,x - 102.95$ and for introduced plants: $y = 1.18\,x - 33.43$. The interaction is significant ($LRT\chi^2 = 12.35$, $df = 1$, $p < 0.001$). The shaded area represents the standard error of the mean. **B** Relationship between leaf-stem biomass (g) and grain yield (g) for *Sonchus oleraceus* populations in the native range (West Palearctic, blue) and in the introduced range (Oceania, orange). Regression estimates for native plants: $y = -0.63\,x + 9.01$ and for introduced plants: $y = -1.27\,x + 10.84$. The interaction is significant ($LRT\chi^2 = 6.81$, $df = 1$, $p < 0.01$). The shaded area represents the standard error of the mean.

of the 20 traits considered either as a main effect or in interaction with range. Shoot height, biomass, LDMC and SDMC increased with minimum temperatures, while germination rate decreased with annual precipitations and temperatures. The height of the introduced plants increased with increasing minimum temperature, whereas no such relationship was observed for native plants. Seed C:N ratio increased with increasing temperature for introduced plants, but decreased with increasing temperature for native plants. Introduced plants tended to display a more rapid decrease in seed production with increasing precipitation than native plants.

Divergence in growth and resource acquisition traits between native and introduced populations

We found that, across all populations (i.e. when the climate experienced by the plant's ancestors was not considered), native and introduced populations differed in terms of vegetative height at first flower bud, biomass, number of leaves and stem dry matter content, with significantly higher values obtained for introduced than for native plants. These results are consistent with those reported for *Centaurea maculosa* (larger and more competitive introduced plants) (Ridenour et al. 2008) and *Silene latifolia* (larger plants in introduced populations) (Blair and Wolfe 2004). However, after considering climatic covariates in the models, we found strong evidence that some trait

divergences for *S. oleraceus* were mediated by climate variation within the native and introduced ranges. We found that minimum temperature had a significant positive effect on several traits across all populations, including plant shoot height, biomass, LDMC of cauline leaf and SDMC. These repeatable trait clines for each range indicate that adaptation to similar selective factors has occurred in native and invaded ranges. Latitudinal gradients in phenological traits are common observations in various geographically widespread plant species (Colautti et al. 2010; Li et al. 2015). For example, it has been shown that SLA of the invasive species *Ambrosia artemisiifolia* had a similar latitudinal cline in the native and the introduced ranges (van Boheemen et al. 2019a). Our results for *S. oleraceus*, in addition to previous studies (e.g. Colautti et al. 2009; Cripps et al. 2010; Alexander et al. 2012), highlight the need to consider climatic variables when investigating phenotypic divergence between native and introduced ranges for invasive plant species, since temperature, precipitation or photoperiod constitute important selective forces driving rapid trait adaptation.

Differential responses to climatic conditions between native and introduced plant populations were also detected for some traits. Specifically, significant interactive effects were observed between range and minimum temperature on vegetative height at first flower bud and seed C:N ratio. Trait values increased with increasing minimum temperature for the introduced plants, whereas no such relationship was observed for native plants. Similarly, a study by van Boheemen et al. 2019a found a differential response to latitudinal cline between native (North American) and introduced (European and Australian) populations for maximum height of the plant *Ambrosia artemisiifolia*. When considering vegetative height at first flower bud for *S. oleraceus*, it could be expected that such trait-climate relationships would be stronger for native populations due to long-term evolutionary adaptations to prevailing environmental selection forces. However, as has been shown in some recent studies (e.g. Smith et al. 2020), genetic structure amongst introduced plant populations is often weaker than amongst native populations due to multiple introductions (whereby propagules are sourced from multiple sites across the native range), resulting in subsequent genetic admixture and expression of novel genotypes. Such novel genotype expression in introduced *S. oleraceus* populations might have resulted in the observed divergence in phenotypic responses to novel climate. Even if no such genetic changes happened during *S. oleraceus* invasion, it is likely that introduced plants grow under novel competitive and environmental (e.g. soil) conditions that may release them from the usual constraints on development and demographic processes. For instance, in the native range, positive effects of temperature on plant height might be offset by commensurate increases in competitive pressures from co-evolved neighbouring plants, yet such competitive pressures on growth may be diluted with increasing temperature if *S. oleraceus* is better able to 'tolerate' competition with its novel neighbours in the introduced range (see discussion by Golivets and Wallin 2018). Although our study has clearly shown patterns of trait divergence between native and introduced plant populations across climate clines, future research on population genetic structure, coupled with climate niche and competition model-

ling, would be required to untangle the mechanisms underpinning such observed patterns (van Boheemen et al. 2019a).

Moreover, even when climate variation was accounted for in the models, we found that the range of origin had a significant effect on cauline leaf dry matter content, number of leaves and stem dry matter content for *S. oleraceus*, indicating that the differences in phenotype between ranges could not be attributed solely to climatic conditions. Similarly, for the introduced *Solidago gigantea*, environmental differences and latitude only explained a small proportion of the total variation observed between the two ranges (Jakobs et al. 2004). The greater number of leaves in introduced *S. oleraceus* populations suggests a greater ability for light interception and photosynthate assimilation. Higher LDMC of cauline leaf and SDMC also indicate that introduced plants invest in a longer life cycle, as dry matter content has been found to be positively related to leaf life span and negatively related to growth rate (Niemann et al. 1992; Ryser 1996; Pérez-Harguindeguy et al. 2013). A higher LDMC has also been observed for the introduced plant *Centaurea stoebe* in North America (Henery et al. 2010). Surprisingly, no significant differences were found for SLA, LDMC or for the thickness and C:N ratio of basal leaves between native and introduced *S. oleraceus* populations. The only significant difference was for the LDMC of cauline leaves. Although we found only moderate trait divergence between native and introduced ranges for *S. oleraceus*, our data still suggest that introduced populations may be evolving a strategy favouring competitive performance of mother plants (i.e. higher leaf and stem dry matter content, larger numbers of leaves) over reproductive output.

There may be several reasons for these observed trait differences. First, maternal effects on plant traits cannot be completely excluded in this study, since the plants were not cultivated in standardised conditions before the experiment. Maternal plants may have experienced variable environmental conditions that influenced growth and resource acquisition traits in the first-generation offspring. However, some studies on different plant species suggest that maternal effects tend to mainly affect early developmental stages and are less pronounced later in the life cycle (Roach and Wulff 1987; Bischoff and Müller-Schärer 2010). Hence, maternal effects might not be responsible for the large differences observed for the latter resource acquisition traits (number of leaves, LDMC of cauline leaf and SDMC). Second, it is possible that populations have indeed undergone rapid post-introduction evolution, as evidenced by trait differences for plants grown under uniform environmental conditions reflecting genetic changes. Rapid evolution is frequently invoked as a reason for phenotypical divergence, for example, in *Leucanthemun vulgare* (Stutz et al. 2018), *Centaurea diffusa* (Turner et al. 2014) and *Arctotheca populifolia* (Brandenburger et al. 2019a, b). In our study, we considered climate as one of the main selective forces shaping trait evolution, but other factors, such as habitat characteristic or soil condition, may also be involved. Third, genetic drift, due to founder effects, could have induced the observed trait differences between native and introduced *S. oleraceus* populations (Bossdorf et al. 2005; van Kleunen et al. 2018). It is possible that the introduced populations were composed of genotypes from the native range already well-adapted to the prevailing climate and

other environmental conditions of the novel range. Furthermore, the likelihood of a bridgehead effect (Bertelsmeier and Keller 2018) and the possibility that European populations selected for comparison did not actually originate from the native area of the plant could be questioned. *Sonchus oleraceus* has been partly characterised genetically (CSIRO 2018). Preliminary analyses showed that diversity in Australia was lower than that in Europe and that Australian samples most likely derived from southern Europe and northern Africa. Considering the extensive occupation of Australia by European descendants since the late 18th century (Cook and Price 1971; van Klinken et al. 2013), a European origin of the plant is the most likely hypothesis. However, to better address this hypothesis, deeper molecular studies would be necessary.

Moderate differences in reproductive but not in phenology and defence traits between native and introduced populations

For reproductive traits, only a few differences were observed between ranges and these differences were contrary to those expected. The main observations concerned the rate of germination after six days. Both climatic covariates, minimum temperature and precipitation, influenced this germination trait. Variations in germination rate along precipitation and temperature gradients are also frequently observed (Gillard et al. 2017; Molina-Montenegro et al. 2018; Yuan and Wen 2018). For example, an increase in germination rate with temperature has been observed in two introduced *Ludwigia* species (Gillard et al. 2017) and three introduced weeds from the Asteraceae (Yuan and Wen 2018). Similarly, an increase in germination rate along a rainfall gradient was shown for *Taraxacum officinale* (Molina-Montenegro et al. 2018). Moreover, for *S. oleraceus*, the rate of germination after six days was significantly higher for introduced plants in models that included climatic covariates. A greater ability to germinate is considered to be an essential life history trait for invasiveness, allowing early access to nutrients, water and space and reducing competition at early stages of establishment (Pyšek and Richardson 2007; Dickson et al. 2012; Gioria et al. 2018). Rapid adaptation of seed germination traits has been shown for the introduced species *Plantago virginica*, which has contributed to its invasion success in China (Xu et al. 2019). Besides climatic conditions, agricultural practices and habitat management could be potential factors of selections in invasive ruderal plant species (Tecco et al. 2010). The reduction of tillage in recent decades, preventing seed burial, may have favoured higher rates of *S. oleraceus* seed germination. Indeed, two studies (i.e. Chauhan et al. 2006; Widderick et al. 2010) have shown that the germination of *S. oleraceus* seeds is greatly decreased by burial at a depth of at least 2 cm.

A significant interaction between range and annual precipitation was also observed for the number of seeds, with introduced plants tending to display a more rapid decrease in seed production with increasing precipitation than native plants, indicating contrasting responses to environmental conditions between native and introduced populations. Similarly, differential trait responses to environmental gradients between

native and introduced populations has been observed for reproductive output in the alien plant *Ambrosia artemisiifolia* (van Boheemen et al. 2019a). One possible explanation for our observation is that *S. oleraceus* adapts to lower drought stress in the introduced range by decreasing its investment in the production of offspring in favour of the establishment of longer-lived mother plants (Jackson and Koch 1997; Grime 2006).

Contrary to our hypotheses, we found no differences in other reproductive traits, phenology or defences against generalist herbivores between native and introduced plants. Release from specialist enemies is thought to lead to strong evolutionary changes within a few generations (Agrawal et al. 2012). Resistance to specialist herbivores would be expected to decrease, whereas resistance to generalist herbivores should increase in introduced populations (Zhang et al. 2018). We have no evidence for these patterns in *S. oleraceus*, as no change in structural defences against generalist herbivores (i.e. leaf trichomes density) was observed. Measurements of the actual damage caused by herbivores in both ranges and the use of a wider range of defence traits, such as secondary metabolite loads, would be required to test this hypothesis more comprehensively (Felker-Quinn et al. 2013).

Shift of the trade-offs between growth and reproduction between native and introduced populations

We found an overall significant positive relationship between vegetative height and number of days to flowering. This likely represents a trade-off between growth and reproductive effort, whereby investment in vegetative tissues, related to growing tall, results in delayed onset of flower production, i.e. short plants flower earlier than tall plants. This relationship is commonly observed for herbaceous plants (Vile et al. 2006; Bolmgren and Cowan 2008; Garnier et al. 2016); however, our study is one of the first to explicitly demonstrate that the pattern of these trade-off relationships can change when a species is introduced to a novel range. A significant difference in the trade-off between vegetative height at first bud and number of days to flowering indicated that introduced plants tended to be taller when they produced their first flowers compared with native plants. Growing taller when initiating flower production may confer competitive benefits for introduced plants relative to neighbouring plants in terms of light acquisition (King 1990; Westoby et al. 2002). Furthermore, for herbaceous plants, being taller at the reproductive stage may improve efficiency of pollination and seed dispersal (Donnelly et al. 1998; Lortie and Aarssen 1999; Soons et al. 2004; Carromero and Hamrick 2005; Thomson et al. 2011).

The overall strong negative relationship between stem-leaf investment and reproductive output confirmed that there is a trade-off between allocation to growth and reproduction, such that larger plants tended to invest relatively less in reproductive output than smaller plants. Trade-offs in growth and reproduction are commonly observed for ruderal plant species (Grime 2006), i.e. short-lived plants growing in marginal, highly disturbed environments with fluctuating resource availabilities. This

trade-off is due to the limited carbon budget that the plant can allocate towards either one of these two strategies under high competition or environmental stress (Reekie and Bazzaz 1987; Stearns 1989; Edward and Chapman 2011). We demonstrated that this growth-reproduction trade-off in *S. oleraceus* differed significantly between native and introduced populations, with a greater investment in plant growth found in introduced compared with native plants for equivalent levels of resource allocated to reproduction. This may represent a fitness benefit for introduced plants along two key niche axes that may explain invasion success (Felker-Quinn et al. 2013). Introduced plants tended to be larger than native plants, suggesting increased competitive abilities and the maintenance of a relatively high grain yield with increasing leaf and stem biomass may favour invasibility through propagule pressure and dispersal opportunities. Similar results (ability to increase population density while sustaining a similar proportion of flowers as native plants) were found for the introduced populations of *Achillea millefolium* in New Zealand (Beckmann et al. 2009) conferring an advantage on introduced plants over native populations.

Conclusion

Our study found that the introduced *S. oleraceus* populations in Australia and New Zealand seem to outperform native populations, by having higher leaf and stem dry matter content, larger number of leaves, greater vegetative height at the early flowering stage, smaller number of seeds and higher germination rate. Shifts in trade-offs for plant height at time of reproduction vs. flowering time and leaves/stems biomass vs. grain yield were observed, suggesting that an ability to adapt life-history traits may also contribute to the invasion success in *S. oleraceus*. We found strong evidence for repeated adaptation to local temperatures and precipitation. When comparing model results with and without climatic covariates, climatic conditions were partly responsible for the observed differences. However, a clear effect of range of origin was observed for some traits, implying a role for other selective factors, such as habitat characteristics, in plant rapid evolution between ranges (Tecco et al. 2010; Colautti and Lau 2015).

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Supplementary material 1

Table S1. Location and climatic data for the 14 *Sonchus oleraceus* populations used for offspring comparisons under standardised conditions

Authors: Melodie Ollivier, Elena Kazakou, Maxime Corbin, Kevin Sartori, Ben Gooden, Vincent Lesieur, Thierry Thomann, Jean-François Martin, Marie Stéphane Tixier

Data type: species data

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Supplementary material 2

Table S2. Mean (± standard error) values for 20 traits assessed for native (Europe and North Africa) and invasive (Australia and New Zealand) populations of *Sonchus oleraceus* under standardised conditions

Authors: Melodie Ollivier, Elena Kazakou, Maxime Corbin, Kevin Sartori, Ben Gooden, Vincent Lesieur, Thierry Thomann, Jean-François Martin, Marie Stéphane Tixier

Data type: species data

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Supplementary material 3

Table S3. Results of mixed models assessing the effect of range (native: Europe and North Africa, introduced: Australia and New Zealand), population within range being considered as a random factor, for 20 plants traits measured on *Sonchus oleraceus* under standardised conditions

Authors: Melodie Ollivier, Elena Kazakou, Maxime Corbin, Kevin Sartori, Ben Gooden, Vincent Lesieur, Thierry Thomann, Jean-François Martin, Marie Stéphane Tixier

Data type: statistical data

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